



Gift carrying in the spider *Pisaura mirabilis*: nuptial gift contents in nature and effects on male running speed and fighting success

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Males of the spider *Pisaura mirabilis* offer prey items as nuptial gifts to females. While gift giving in this species has received attention in captivity, the ecological context of these gifts remains largely unknown. First, we examine the occurrence of gift carrying by males in nature. Field data reveal that gift-carrying males are frequent in nature (40% of captured males), and that all gifts contain fresh arthropod prey. Gift mass was positively correlated with the longest diameter of the gift. Thus, males do not appear to ‘cheat’ by inflating their gifts with inedible items, air or loosely wrapped silk. Second, we examine two ecological costs to gift-carrying males: the effects of gifts on male running speed and male fighting success. Gift carrying reduced male running speed, but did not affect male fighting success in male–male contests. The former result is the first demonstration of a transportation cost associated with gift carrying in an arthropod.

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In many arthropods, males provide nuptial gifts to females, which can consist of captured food, glandular or salivary secretions, spermatophores, or the male's body parts (reviewed in: [Simmons & Parker 1989](#); [Vahed 1998, 2007](#); [Gwynne 2008](#)). The evolution of nuptial gifts can lie in a combination of fitness benefits to the male, such as increased mating success and/or increased paternal investment (increase the quality and quantity of his offspring), and to the female, in the form of nutrition used to increase female fitness and/or offspring quality and probability of survival ([Simmons & Parker 1989](#); [Vahed 1998, 2007](#)).

While nuptial gifts can offer benefits to male and female fitness, they involve costs to both sexes as well. The particular form of the cost will often depend on the form of the donation itself. In some species, the costs of donations are quite obvious to the male, such as gryllid crickets in which the female chews and consumes a male body part, typically reducing the male's future reproductive success ([Fedorka & Mousseau 2002](#); [Sakaluk et al. 2004](#); [Piascik et al. 2010](#)). A more extreme nuptial offering can be found in the males of the

Australian redback spider, *Latrodectus hasselti*, which somersault into the females' mouthparts during copulation, risking death for the sake of prolonging copulation ([Andrade 1996](#)). In other species, donations are energetically costly, such as large spermatophores produced by male tettigoniids ([Simmons 1990](#); [Simmons & Gwynne 1991](#); [Wedell 1994](#); [Vahed 2007](#)).

In some arthropods, males carry gift items as they search for or court females. This form of nuptial gift occurs in dance flies (Diptera: Empididae), hangingflies and scorpionflies (Mecoptera), and some spiders ([Bristowe 1968](#); [Austad & Thornhill 1986](#); [Vahed 1998](#); [Costa-Schmidt et al. 2008](#)). These gifts are often procured before the male contacts the female ([Nitzsche 1988](#)), requiring the male to retain and carry the item in his travels. In these species, then, the gift item may pose ecological costs for males, including movement costs and possible lost opportunities for feeding. In the context of courtship, gift items carried by male dance flies may reduce manoeuvrability or flight efficiency for the males ([Sadowski et al. 1999](#); [LeBas et al. 2004](#)). With regard to travel involved in searching for females, the effects of gift transport on male behaviours, such as movement and intermale competition, have eluded experimental examination in gift-giving arthropods.

We examine the ecological costs of gift carrying to males in the spider *Pisaura mirabilis*. In this spider, males wrap prey items in silk, hold them with their chelicerae, and offer the items to females. The

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female may accept the item into her chelicerae; as she feeds, the male transfers sperm (Austad & Thornhill 1986; Stålhandske 2001a, b). Previous research demonstrates the importance of possessing a gift to male mating success in this species. In some populations, females appear to require the prey item for insemination to occur (Austad & Thornhill 1986; Prokop & Maxwell 2009). Copulation duration increases with gift size and, in turn, copulation duration positively correlates with fertilization success (Stålhandske 2001a). It is suspected that males carry gift items in the field as they search for females (Nitzsche 2011), as in other gift-giving spiders (Costa-Schmidt et al. 2008; Albo et al. 2009).

Despite these benefits to male mating success, the gifts' costs to males remain poorly understood. For example, authors differ on whether silk production and gift wrapping are energetically costly (Lang 1996; Albo et al. 2011a), and costs associated with gift carrying have not been examined. The present study examines ecological costs associated with gift carrying. First, we investigate the incidence of male gift carrying in nature, to document this behaviour and to describe the characteristics and contents of field-collected gifts. We are particularly interested in whether males 'inflate' the gifts by adding inedible items as a possible way of reducing the effort involved in acquiring prey to package as gifts, as suggested by some authors (Nitzsche 2011; Albo et al. 2011b). Second, we examine the effects of gift carrying on two male behaviours: running speed and male–male fights. *Pisaura mirabilis* is a ground-dwelling spider, and males are commonly found crawling on the ground or on vegetation in nature (P. Prokop, personal observation). We ask whether male running speed is affected by holding a gift item. With regard to male–male fights, such fights are common in captive colonies (Nitzsche 2011), and are expected to occur in nature (Nitzsche 1988). We therefore ask whether possession of a gift confers an advantage or a disadvantage to the male in combat.

METHODS

Study Organism

The nursery-web spider, *Pisaura mirabilis* (Pisauridae), is a predominantly diurnal predator (Nitzsche 2011), living in grasslands and deciduous woods. Its life cycle is annual in central Europe (Buchar et al. 1989). Spiderlings hatch in late June–August and reach maturity in April–May of the following year. Mature males can be found until June, whereas females may be seen into late summer (P. Prokop, personal observation). When a male detects a receptive female's draglines, he catches a prey item and wraps it with silk (e.g. Nitzsche 1988; Albo et al. 2011a). Males have also been observed to wrap prey and carry it as a nuptial gift soon after final moult, even in the absence of a female (Lang 1996; P. Prokop, personal observation), which allows a male to court a female upon detecting her (Albo et al. 2011a). The male then approaches the female, and the female seizes the gift. Once the female holds the gift in her chelicerae, the male swivels around and positions himself underneath the female's sternum, facing away from her anterior. While the female feeds on the gift item, the male inserts his pedipalp into the female's epigyne and transfers sperm.

Nuptial Gifts in the Field

To examine the contents of nuptial gifts in the field, we randomly captured 58 adult males through visual searching at two open woodland sites near Trnava, Slovakia (48°23'N, 17°35'E) during 8–14 May 2010. Early May is typically the peak mating season for *P. mirabilis* in Slovakia (P. Prokop, unpublished data), when males are most likely to be found carrying gifts in the field.

Searching and capture occurred during daylight hours (1300–1700 hours). Upon capture, each male was isolated in a ventilated cup (0.3 litre) with wet cotton to maintain humidity. Each male was anaesthetized soon after capture, and the gifts were carefully removed from the males' chelicerae to avoid consumption of the gifts. Gifts were weighed to 0.0001 g, and measured along the longest diameter to 0.01 mm. The contents of the gifts were then examined through dissection under a binocular microscope. On the following morning, each male was anaesthetized with CO₂, and prosoma width (to 0.01 mm) and body mass (to 0.0001 g) were measured. Throughout this study, we quantified male body condition as the residual of regression of body mass on prosoma width (Jakob et al. 1996). After all measurements, the spiders were returned to their sites of capture. These releases occurred after all spiders had been captured, so no male was captured more than once. All field work and experiments were performed in compliance with Slovakian laws.

Ecological Costs of Nuptial Gifts: Male Running Speed and Male–Male Fights

To examine ecological costs of nuptial gifts, we captured 125 subadult males from mixed woodlands near Trnava in April 2010. Each juvenile was isolated in a ventilated 0.3-litre glass jar provided with wet cotton, maintained at 20 °C, and exposed to natural photoperiod. The spiders were fed house cricket nymphs (*Gryllus assimilis*) three times per week (ca. five crickets per feeding), and were misted with water once per day. Each juvenile was checked daily for adult emergence; 119 subadults became adults. Adult males were fed daily with cricket nymphs on an ad libitum basis. Trials that examined running speed and male–male fights were conducted indoors, 20 °C, and exposed to indirect sunlight. From our field collections, we observed males actively crawling and carrying gifts during the day. Nuptial gifts used in the trials were freshly killed crickets (by CO₂) of standardized size (random sample of crickets: mean \pm SE = 0.014 \pm 0.0005 g, N = 10), being of comparable size to gift items used in other studies on *P. mirabilis* (e.g. range 2.3–29.1 mg, Stålhandske 2001a; mean = 15.5 mg, Stålhandske 2002; mean = 11.9 mg, Prokop & Maxwell 2009), as well as gift items reported from nature (Nitzsche 1988; Stålhandske 2001a, b; this study).

Effect of nuptial gifts on male running speed

For trials to test running speed, we randomly selected 10 adult males (mean mass \pm SE = 0.0984 \pm 0.007 g; mean prosoma width \pm SE = 3.58 \pm 0.12 mm; N = 10). Each male was 10–12 days postemergence. Each male was tested in two trials: one trial with a gift item (freshly killed cricket nymph: mean \pm SE = 0.0250 \pm 0.0002 g, N = 10), and the other trial without a gift item. Five of the males performed the trial with the gift first, followed by the trial without a gift. The other five males did the trials in reverse order.

Trials were conducted indoors between 1100 and 1300 hours. For each trial, the male was placed at one end of a wooden stick (1 m long, 2 cm diameter) that was fixed 15 cm above a horizontal surface. The stick was surrounded by white paper to reduce visual distractions to the spider. If the trial involved running with the gift, we first released the male in a glass terrarium (30 \times 20 \times 20 cm) lined with white paper that a virgin female had previously crawled on for 10 min. Female draglines induce male sexual behaviour (e.g. Nitzsche 1988; Stålhandske 2001a, b; Albo et al. 2011a) and stimulate males to wrap prey items with silk. We provided the cricket to the male in the terrarium. Once the male had wrapped the cricket in silk and held it in his chelicerae, we placed him on the stick. The

trial began by inducing the male to run by gently touching his dorsal opisthosoma with soft tweezers. This encouraged the male to run continuously without stopping during the trial. The time taken for the male to run the entire length of the stick was recorded (to 1 s). Once the male completed a trial, he was kept in his home container for 10 min, and then run through his second trial. Trials without gift items were conducted as for trials with gifts, wherein the male was released in the glass terrarium for 10 min, then placed on the 1 m stick and gently touched on the dorsal opisthosoma to induce running.

Effect of nuptial gifts on male–male fights

For trials to examine male–male fights, we randomly selected 94 adult males that were 10–12 days postemergence. We paired males for fighting trials ($N = 47$ trials in total), matching the males in terms of body mass, prosoma width and body condition (paired t tests: body mass: $t_{44} = 0.32$, $P = 0.75$; prosoma width: $t_{44} = 1.69$, $P = 0.1$; body condition: $t_{44} = 0.75$, $P = 0.45$). Each pair of males was randomly assigned to one of three treatments: one male was randomly provided a gift item (cricket) while the other male was not provided with a gift (GN treatment, $N = 17$ trials), neither male was provided a gift (NN treatment, $N = 15$ trials), and both males were provided a gift (GG, $N = 15$ trials). This allowed for comparing the effects of carrying gift items. Within the GN treatment, the male that was provided with a gift was of similar body mass, prosoma width and body condition to the other male (paired t tests: body mass: $t_{16} = -0.16$, $P = 0.82$; prosoma width: $t_{16} = -1.25$, $P = 0.24$; body condition: $t_{15} = 0.95$, $P = 0.3$).

Fight trials were based on methods described in Kotiaho et al. (1999) for male–male contests in wolf spiders. Trials were conducted indoors 4–12 May 2010, between 1000 and 1500 hours. Each trial occurred in a glass terrarium ($30 \times 20 \times 20$ cm) that was lined with clean white paper. Before males were placed into the terrarium, a well-fed virgin female (10–20 days postemergence) was allowed to crawl in the terrarium for 20 min, setting down draglines to stimulate male courtship and gift construction. The female was then placed in a ventilated cube (44.5 mm per side) at the centre of the terrarium. The cube was covered with fine mesh (mesh size: 1.3×1.3 mm), allowing for visual and olfactory contact between the female and the two males. Three different virgin females were used in the 47 trials, being randomly selected for use in a given trial.

Before placement into the terrarium, each paired male was briefly anaesthetized with CO_2 and measured for body mass and prosoma width. Each male was individually marked with white paint on the dorsal side of the prosoma. After recovering from anaesthesia, the males were then released simultaneously at the opposite sides of the terrarium. At the time of release, a paper strip divided the terrarium in half, to initially separate the males. The female was randomly placed to the right or left of this strip. During this initial separation, a cricket gift item was quickly provided to selected males in the GN and GG treatments. All males grabbed the item with their chelicerae within 60 s after the gift's introduction. The paper strip was removed 1–2 s after one male (GN treatment) or both males (GG treatment) grabbed the prey item. The males were allowed 15 min to interact, during which time their behaviours were recorded. We recorded latency to first contact between the males, the occurrence of fights (where a fight is a short bout, up to 5 s, of physical grappling and biting attempts directed at the legs of the rival male) and the loser of each fight. In *P. mirabilis*, the loser of a male–male fight is obvious, as he quickly runs away after short physical combat (Nitzsche 2011). The dominant male for a trial was determined as the winner of the majority of fights (more than 50%); the other male was termed subordinate. To analyse latency time until first physical contact between males, Kaplan–Meier survival

curves were computed for less than 95% adherence and 95% or greater adherence, and were compared by the Mantel–Cox test.

Statistical Analyses

Statistical tests were performed with Statistica (v8, StatSoft 2007, Tulsa, OK, U.S.A., <http://www.statsoft.com>). All the variables and relationships were checked for normality to perform parametric tests. All tests were two-tailed. For descriptive statistics, means are reported with standard errors (SE).

RESULTS

Nuptial Gifts in the Field

Of the 58 captured males, 23 were carrying silk-wrapped gifts upon discovery in the field. All gifts contained the bodies of arthropods. The prey bodies were chewed and broken apart, which did not allow for deeper taxonomic identification. We found no desiccated prey, or empty, dry exoskeletons in the males' gifts. Rather, the contents of the gifts looked to be fairly recent kills that were fresh and edible. The gifts' longest diameter (mean \pm SE = 3.18 ± 0.17 mm, range 2.02–4.70) and mass (mean \pm SE = 0.0096 ± 0.0016 g, range 0.0018–0.0271) were significantly correlated (Pearson correlation: $r_{21} = 0.77$, $P < 0.001$).

Males with and without gifts did not differ significantly in body mass (paired t test: $t_{56} = 1.34$, $P = 0.16$), prosoma width ($t_{56} = 0.95$, $P = 0.35$) or body condition ($t_{56} = 0.97$, $P = 0.34$). For males with gifts, there was no correlation between gift mass and body mass (Pearson correlation: $r_{21} = 0.027$, $P = 0.9$), prosoma width ($r_{21} = 0.058$, $P = 0.79$) or body condition ($r_{21} = -0.04$, $P = 0.85$).

Ecological Costs of Nuptial Gifts: Male Running Speed and Male–Male Fights

Effect of nuptial gifts on male running speed

When carrying nuptial gifts, males showed some effects of load, veering from side to side more so than when they were not carrying gifts. All males retained their grip of the gift while running; no males dropped the gift. Males with gifts ran more slowly, taking significantly more time to run across the 1 m stick than when running without gifts (paired t test: $t_9 = 6.88$, $P < 0.001$; Fig. 1).

Effect of nuptial gifts on male–male fights

At least one fight occurred between the paired males in all 47 trials (mean \pm SE fights per trial = 4.30 ± 0.42 , range 1–12 fights per trial). Fights were typically short, usually grappling bouts of 5 s or less. The number of fights per trial did not significantly differ between treatments (ANOVA: $F_{2,44} = 0.43$, $P = 0.66$; Table 1). Thus, the presence or absence of the nuptial gift did not affect the number of fights within a trial.

Mean latency to fight was 158 s (SE = 19.9, $N = 47$ trials). Latency to fight did not significantly differ between treatments, either by survival analysis (Mantel–Cox test: $\chi^2_2 = 1.23$, $P = 0.54$) or by ANOVA (log($x+1$)-transformed data: $F_{2,44} = 1.21$, $P = 0.31$). In 45 trials where the dominant male was clearly distinguishable, the dominant male won an average of 99.8% of the fights (range 90–100%). In the remaining two trials (one GG, one GN), a dominant male could not be assigned, as both males won 50% of fights. Across all treatments, dominant males did not differ from subordinate males in body condition (Table 1).

Examining the effect of nuptial gifts on fights in the GN treatment (one male with gift, the other male without), nine of the 16 males with the nuptial gift were the dominant males (binomial test: $P = 0.80$), suggesting that having a gift had little effect on fight

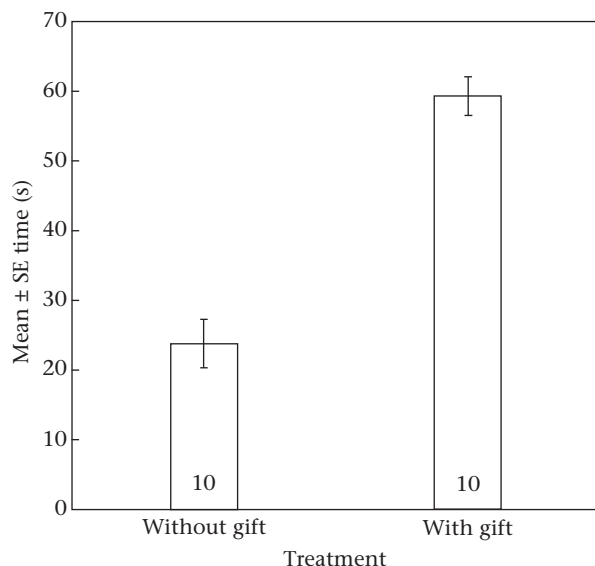


Figure 1. Time that males with and without a nuptial gift took to run across a 1 m stick. Numbers in bars are sample sizes.

outcomes. In these 16 GN trials, the dominant male and subordinate male did not significantly differ in body condition (paired t test: $t_{15} = 1.90$, $P = 0.08$).

Male 'theft' behaviour suggests high value for the nuptial gifts. In the GN treatment, five dominant males without gifts took the nuptial gift from the subordinate (i.e. 5 of 16 trials, 31%). Similarly, two dominant males in the GG treatment (both males with gifts) took the nuptial gift from the subordinate.

DISCUSSION

The present study reveals an ecological cost of gift carrying in the spider *P. mirabilis* males. Gift carrying by males reduced male running speed. This is the first demonstration of a transportation cost associated with gift carrying in an arthropod. *Pisaura mirabilis* males appear to search for females while clutching wrapped gifts (Nitzsche 1988; this study). Given that females require a gift item for copulation to occur in our study populations (Prokop 2006; Prokop & Maxwell 2009; but see Stålhandske 2001a; Nitzsche 2011), the benefits of having a gift item at the ready when encountering a female in the field presumably compensates for any costs incurred while gift carrying to some degree (Albo et al. 2009). Such costs may involve increased energy expenditure and increased vulnerability to predators. Gifts carried by males in the field in the present study (mean = 0.0096 g, maximum = 0.0271 g) were of comparable mass to gifts found to decrease male speed in captive trials (mean = 0.014 g). Survival costs imposed by gift carrying deserve further attention in *P. mirabilis* and other gift-carrying spiders. An analogous cost has been identified in females

of the wolf spider *Pardosa milvina*, where females carrying eggsacs experience significantly greater predation than females without eggsacs, most likely due to decreased locomotory efficiency (Colancecco et al. 2007).

Nuptial gifts in *P. mirabilis* may involve physiological or energetic costs in their construction, although researchers are divided on this issue. Males do not always wrap gifts with silk before presenting them to females, yet females will accept unwrapped gifts (Lang 1996; Bilde et al. 2007; Albo et al. 2011a; P. Prokop, unpublished data). Lang (1996) concluded that silk production to wrap gift items posed negligible costs to males. Albo et al. (2011a), however, found that males in good feeding condition spent more time on gift construction and used more silk than males in poor feeding condition, suggesting a physiological or energetic cost to gift construction.

Despite the potential costs imposed by the construction and transportation of nuptial gifts in *P. mirabilis*, the present study indicates that the gifts are nutritious offerings and possible honest indicators of male foraging success (Thornhill 1976; Zahavi & Zahavi 1997; Vahed 1998; Gwynne 2008). In the present study, all gifts found in nature contained arthropod prey, and the longest diameter strongly correlated with gift mass. Thus, the males do not appear to 'cheat' by inflating the gifts with air, inedible items or loosely wrapped silk (Bristowe 1968; Stålhandske 2002; Nitzsche 2011). Albo et al. (2011b) similarly dissected 16 gifts collected from *P. mirabilis* males in the field. Interestingly, they found that 62% of the gifts held fresh prey, while the remaining 38% held empty arthropod skeletons of presumably low nutritional value. Whether these empty skeletons resulted from the gradual desiccation of high-quality wrapped prey items, the male's wrapping of low-quality prey items, or the male's sucking of fluid from wrapped high-quality items is unknown. While the last two possibilities suggest a certain degree of male deception in gift construction, Albo et al. (2011b) reported shorter copulation durations for males that provided low-quality gifts to females in captive trials (i.e. gifts consisting of wrapped cotton or prey remains). Shorter copulation duration for low-quality gifts seems to be a female counterstrategy that would select for males that provide gifts of high quality.

In addition to male foraging success, the gift might reflect the male's resource holding ability in a quite literal sense (Parker 1974; Arnott & Elwood 2008). While the possession of a gift item conferred neither an advantage nor a disadvantage in male–male fights in the present study (see Sadowski et al. 1999 for dance flies), 'theft' attempts by males occurred with some frequency, particularly in trials in which one male had a gift and the other male did not (cf. Nitzsche 2011). Thus, the male's presentation of a gift to the female may indicate his quality, both in terms of foraging and in his ability to retain the gift in the face of environmental hazards and conspecific competitors. Clearly, examinations of intermale fights and contests in nature are required to evaluate the notion of the gift as a reflection of the male's resource holding ability.

In summary, this study indicates an ecological cost to gift carrying in the spider *P. mirabilis*: reduced running speed. The nuptial gifts appear to be nutritious offerings in nature, containing edible arthropod prey, and potentially honest indicators of male

Table 1
Results of male–male fights in nursery-web spiders

Treatment	Mean ± SE number of fights per trial	Mean ± SE body condition of dominant male	Mean ± SE body condition of subordinate male	Body condition of dominant and subordinate males within a trial (paired t test)
NN ($N=15$)	3.73±0.76	0.004±0.003	−0.0008±0.003	$t_{14}=1.58$, $P=0.14$
GG ($N=15$)*	4.67±0.76	−0.002±0.003	0.003±0.003	$t_{13}=1.29$, $P=0.22$
GN ($N=17$)*	4.47±0.71	−0.0003±0.002	−0.005±0.002	$t_{15}=1.90$, $P=0.08$

NN: neither male had a gift item; GG: both males had a gift item; GN: one male had a gift item.

* One trial was excluded for calculation of mean winner and loser condition (see text).

qualities such as foraging ability. Given that the gift confers known benefits to male fitness in this species (e.g. Stålhandske 2001a; Prokop & Maxwell 2009), further examinations of the costs involved in the construction and transportation of the gifts will shed light on their evolution.

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References

- Albo, M. J., Costa-Schmidt, L. E. & Costa, F. G. 2009. To feed or to wrap? Female silk cues elicit male nuptial gift construction in the spider *Paratrechalea ornata* (Trechaleidae). *Journal of Zoology*, **277**, 284–290.
- Albo, M. J., Toft, S. & Bilde, T. 2011a. Condition dependence of male nuptial gift construction in the spider *Pisaura mirabilis* (Pisauridae). *Journal of Ethology*, **29**, 473–479.
- Albo, M. J., Winther, G., Tunī, C., Toft, S. & Bilde, T. 2011b. Worthless donations: male deception and female counter play in a nuptial gift-giving spider. *BMC Evolutionary Biology*, **11**, 329.
- Andrade, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271**, 70–72.
- Arnott, G. & Elwood, R. W. 2008. Information gathering and decision making about resource value in animal contests. *Animal Behaviour*, **76**, 529–542.
- Austad, S. N. & Thornhill, R. 1986. Female reproductive variation in a nuptial-feeding spider, *Pisaura mirabilis*. *Bulletin of the British Arachnological Society*, **7**, 48–52.
- Bilde, T., Tunī, C., Elsayed, R., Pekár, S. & Toft, S. 2007. Nuptial gifts of male spiders: sensory exploitation of the female foraging motivation. *Animal Behaviour*, **73**, 267–273.
- Bristowe, W. S. 1968. *The Comity of Spiders*. London: Johnson Reprint.
- Buchar, J., Babrakzai, H. & Hodek, I. 1989. Life-cycle and phenology of the spider *Pisaura mirabilis* (Araneae) in central Europe. *Acta Entomologica Bohemoslovaca*, **86**, 414–418.
- Colanecceco, M., Rypstra, A. L. & Persons, M. H. 2007. Predation and foraging costs of carrying eggsacs of different mass in the wolf spider *Pardosa milvina*. *Behaviour*, **144**, 1003–1018.
- Costa-Schmidt, L. E., Carico, J. E. & Araújo, A. M. 2008. Nuptial gifts and sexual behaviour in two species of spider (Araneae, Trechaleidae, Paratrechalea). *Naturwissenschaften*, **95**, 731–739.
- Fedorka, K. M. & Mousseau, T. A. 2002. Tibial spur feeding in ground crickets: larger males contribute larger gifts (Orthoptera: Gryllidae). *Florida Entomologist*, **85**, 317–323.
- Gwynne, D. T. 2008. Sexual conflict over nuptial gifts in insects. *Annual Review of Entomology*, **53**, 83–101.
- Jakob, E. M., Marshall, S. D. & Uetz, G. W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**, 61–67.
- Kotiaho, J. S., Alatalo, R. V., Mappes, J. & Parri, S. 1999. Honesty of agonistic signalling and effects of size and motivation asymmetry in contests. *Acta Ethologica*, **2**, 13–21.
- Lang, A. 1996. Silk investments in gifts by males of the nuptial feeding spider *Pisaura mirabilis* (Araneae: Pisauridae). *Behaviour*, **133**, 697–716.
- LeBas, N. R., Hockham, L. R. & Ritchie, M. G. 2004. Sexual selection in the gift-giving dance fly, *Rhamphomyia sulcata*, favors small males carrying small gifts. *Evolution*, **58**, 1763–1772.
- Nitzsche, R. O. M. 1988. 'Brautgeschenk' und Umspinnen der Beute bei *Pisaura mirabilis*, *Dolomedes fimbriatus* und *Thaumasia uncuta* (Arachnida, Araneida, Pisauridae). *Verhandlungen des Naturwissenschaftlichen Vereins zu Hamburg*, **30**, 353–393.
- Nitzsche, R. O. M. 2011. Courtship, mating and agonistic behaviour in *Pisaura mirabilis* (Clerck, 1757). *Bulletin of the British Arachnological Society*, **15**, 93–120.
- Piasek, E. K., Judge, K. A. & Gwynne, D. T. 2010. Polyandry and tibial spur chewing in the Carolina ground cricket (*Eunemobius carolinus*). *Canadian Journal of Zoology*, **88**, 988–994.
- Parker, G. A. 1974. Assessment strategy and evolution of fighting behavior. *Journal of Theoretical Biology*, **47**, 223–243.
- Prokop, P. 2006. Insemination does not affect female mate choice in a nuptial feeding spider. *Italian Journal of Zoology*, **73**, 197–201.
- Prokop, P. & Maxwell, M. R. 2009. Female feeding regime and polyandry in the nuptially-feeding nursery web spider, *Pisaura mirabilis*. *Naturwissenschaften*, **96**, 259–265.
- Sadowski, J. A., Moore, A. J. & Brodie, E. D. 1999. The evolution of empty nuptial gifts in a dance fly, *Empis snoddyi* (Diptera: Empididae): bigger isn't always better. *Behavioral Ecology and Sociobiology*, **45**, 161–166.
- Sakaluk, S. K., Campbell, M. T. H., Clark, A. P., Chadwick-Johnson, J. & Keorpes, P. A. 2004. Hemolymph loss during nuptial feeding constrains male mating success in sagebrush crickets. *Behavioral Ecology*, **15**, 845–849.
- Simmons, L. W. 1990. Nuptial feeding in tettigoniids: male costs and rates of fecundity increase. *Behavioral Ecology and Sociobiology*, **27**, 43–47.
- Simmons, L. W. & Gwynne, D. T. 1991. The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the remating interval? *Behavioral Ecology*, **2**, 276–282.
- Simmons, L. W. & Parker, G. A. 1989. Nuptial feeding in insects: mating effort versus paternal investment. *Ethology*, **81**, 332–343.
- Stålhandske, P. 2001a. Nuptial gift in the spider *Pisaura mirabilis* maintained by sexual selection. *Behavioral Ecology*, **12**, 691–697.
- Stålhandske, P. 2001b. Male and female reproductive strategies in the nursery web spider *Pisaura mirabilis*. Ph.D. thesis, Göteborg University.
- Stålhandske, P. 2002. Nuptial gifts of male spiders function as sensory traps. *Proceedings of the Royal Society B*, **269**, 905–908.
- Thornhill, R. 1976. Sexual selection and paternal investment in insects. *American Naturalist*, **110**, 153–163.
- Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biological Reviews*, **73**, 43–78.
- Vahed, K. 2007. All that glitters is not gold: sensory bias, sexual conflict and nuptial feeding in insects and spiders. *Ethology*, **113**, 105–127.
- Wedell, N. 1994. Dual function of the bushcricket spermatophore. *Proceedings of the Royal Society B*, **258**, 181–185.
- Zahavi, A. & Zahavi, A. 1997. *The Handicap Principle: a Missing Piece of Darwin's Puzzle*. Oxford: Oxford University Press.